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ORIGINAL PAPER

Covariance between disturbance and soil resources dictates the invasibility of northern fescue prairies

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Abstract Increasing environmental impacts of exotic organisms have refocused attention on the ability of diverse communities to resist biological invaders. Although resource availability, often related to natural and anthropogenic disturbances, appears central to the invasibility of biological communities, understanding the links between resources, diversity and invasibility is often confounded by the covariance among key variables. To test the hypothesis that community invasibility remains contingent on the type and intensity of disturbance and their impacts on plant community diversity and resource availability, we designed an experiment testing the invasibility of northern fescue prairies by smooth brome (*Bromus inermis* Leyss.), a Eurasian perennial grass, threatening the structure and function of prairie remnants throughout the Great Plains. Using soil disturbances and herbicide, we imposed treatments manipulating the diversity and resource availability of native prairies. Our observations demonstrate that the vulnerability of native prairies to exotic plant invasions remains contingent on resources. While the establishment of smooth brome seedlings increased with increasing disturbance, its impact depended on the availability of soil nitrogen. As a result, soil burial treatments, simulating disturbance by northern pocket gophers, provided poor recruitment areas for smooth brome, and their low levels of soil moisture and nitrogen, combined with the rapid recovery of the prairie community, compromised seedling establishment. Emphasizing the covariance of diversity and key environmental variables following disturbance, our findings illustrate the importance of disturbance type and intensity on community invasibility. Such a consideration is critical in the conservation and restoration of native prairie remnants throughout the Great Plains.

Keywords Invasion resistance · Disturbance · Community diversity · Invasive species · *Bromus inermis* · Smooth brome · Native prairie

Introduction

The sustained loss of global biodiversity stimulates intense debate regarding its role in ecosystem function (Chapin et al. 1998; McCann 2000). Recent work, motivated by the increasing environmental impacts of

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exotic organisms (Mack et al. 2000; Ricciardi 2007), has centered on the ability of diverse communities to resist biological invaders (Kennedy et al. 2002). Despite the relevance of the diversity–stability hypothesis to the conservation and restoration of natural communities, experimental results have been mixed (Levine and D'Antonio 1999; Wardle 2001). For example, studies exploring links between diversity and invasibility have revealed both positive (Lonsdale 1999; Stohlgren et al. 1999; McKinney 2002; White and Houlahan 2007) and negative (Tilman 1997; Knops et al. 1999; Levine 2000; Naeem et al. 2000; Kennedy et al. 2002; Biondini 2007) relationships, while others have been inconclusive (Crawley et al. 1999; Collins et al. 2007; Mattingly et al. 2007). Despite these inconsistencies, the majority of studies consider resource availability central to the invasibility of biological communities (Levine and D'Antonio 1999; Davis et al. 2000). While species richness often increases the utilization of resources (Tilman et al. 1997; Shea and Chesson 2002; Verheyen et al. 2008), the establishment of potential invaders may depend more on spatial and temporal fluctuations in resources than on community diversity (Burke and Grime 1996; Wardle 2001; Kolb et al. 2002; Melbourne et al. 2007). These, often exacerbated by natural and anthropogenic disturbances, are likely important catalysts for invasion (Fox and Fox 1986; Hobbs and Huenneke 1992; Wardle 2001; McCann 2007).

Understanding the links between diversity and invasibility is often confounded by the covariance among key variables (Levine and D'Antonio 1999; Lamb 2008). These 'hidden treatments', resulting from interactions among several variables following experimental manipulation, can confound the interpretation of results (Huston 1997). For example, disturbances that alter community diversity, including fire and herbivory, also frequently alter the availability of resources (Mack 1989; D'Antonio and Vitousek 1992). As a result, their impacts on community architecture and trophic structure (Mack et al. 2000; McCann 2007), functional complementarity (Prieur-Richard et al. 2002; Shipley et al. 2006; Biondini 2007), and the physical and chemical elements of environments (Lake and Leishman 2004), may also create establishment opportunities for potential invaders.

Natural disturbances, including fire, grazing, and the burrowing of fossorial mammals are integral to the structure and function of prairie and grassland ecosystems (Martinsen et al. 1990; Collins and Steinauer 1998). Despite their role in creating niche opportunities for potential invaders (Parker et al. 1993), differences in the type and intensity of disturbance suggest important distinctions in their impact on community invasibility (Vujnovic et al. 2002; Gibson 1989). For example, the large belowground biomass of most prairie plants (Tilman et al. 1996; Rice et al. 1998) suggests that communities characterized by the loss of aboveground biomass only, should continue to resist potential invaders. By limiting the niche opportunities available to invaders, the persisting roots and rhizomes of resident species should continue to resist their establishment (Crowley et al. 2005).

To test this hypothesis, we explored the impacts of disturbance type and intensity on the invasibility of northern fescue prairies. Using soil disturbances, designed to simulate the impacts of northern pocket gophers (*Thomomys talpoides*), as well as applications of herbicide, we explored the impact of disturbance on the establishment of *Bromus inermis* Leyss., a Eurasian perennial grass threatening the structure and function of prairie remnants throughout the Great Plains (Otfinowski et al. 2007). Unlike the burial caused by pocket gophers, which preserves the roots and rhizomes of resident species (Laycock 1958; Foster and Stubbendieck 1980; Gibson 1989), applications of systemic herbicide eliminate both their above- and belowground biomass (Grangeot et al. 2006). Using both manipulations, we tested the hypothesis that community invasibility remains contingent on the type and intensity of disturbance and their impacts on plant community diversity and resource availability.

Methods

Research was conducted in Riding Mountain National Park, Manitoba, Canada. The park occupies an area of 2,978 km^2 in Western Canada, 225 km northwest of Winnipeg (49°53′04″N–97°08′47″W) and consists of large areas of rolling upland (550–640 m), underlain by glacial tills (Lang 1974). The region is characterized by mean annual precipitation of 450–500 mm and a growing season of 168–173 days; mean temperatures range between -18°C in January and 18°C during July (Leeson et al. 2005). The park lies in the Mixedwood Section of the Boreal Forest Region (Rowe 1972) and protects areas of northern fescue prairie, threatened in western Canada by grazing, cultivation, and invasions of exotic species (Trottier 1986).

To examine the impact of disturbance type and intensity on the invasibility of northern fescue prairies, we selected three experimental blocks (8 × 5 m) in each of two prairies located in the park. The two study areas were situated approximately 50 km apart; soils at the more western Bob Hill prairie were more xeric and lower in mineral nitrogen than the centrally located Strathclair prairie [moisture (0–20 cm, July 2005) 7.5 ± 3.7 vs. 9.5 ± 4.2%, $F_{1,100} = 9.2$, $P = 0.0031$; mineral nitrogen (0–15 cm; July 2005): NH_4^+, 5.3 ± 0.4 vs. 9.1 ± 0.4 mg/kg, $F_{1,38} = 37.4$, $P < 0.0001$; NO_3^-, 0.60 ± 0.1 vs. 2.1 ± 0.2 mg/kg, $F_{1,38} = 40.7$, $P < 0.0001$].

We examined the impacts of disturbance on plant community invasibility by manipulating the structure and composition of native prairies. Based on a simple randomized block design, we divided each experimental block into six quadrats (2 × 2 m) and randomly assigned treatments to the four 1 × 1 m cells inside each quadrat (Fig. 1). Starting in July 2003, one moderate and two high disturbance treatments were applied to 60 × 60 cm areas at the center of each cell. Inside the moderate disturbance treatments, we used foam brushes to apply a 33% glyphosate:water solution (Vantage Plus, Dow AgroSciences Canada, Calgary, AB) to the leaf surfaces of forbs. In the first high disturbance treatment, we used the same herbicide to target all resident plants; in the second, we focused our disturbance aboveground by burying all vegetation inside a treatment cell with loose soil. Soil (24 L) was collected from nearby pocket gopher mounds and used to simulate their impact on prairie communities. The fourth cell was left untreated as a control.

We quantified the invasibility of disturbed prairies using transplants of *Bromus inermis*. Starting in May 2004, four *B. inermis* seedlings (Carlton; Brett-Young seeds, Winnipeg, MB) were transplanted inside a 20 × 20 cm area at the center of each treatment area (Fig. 1). Seedlings were germinated and raised in root trainers in a greenhouse (day: 16 h/21°C; night: 8 h/15°C) and cold hardened at the five-leaf stage (height < 9 cm, <1 tiller), 1 week prior to transplanting. We used a hand auger to extract cores

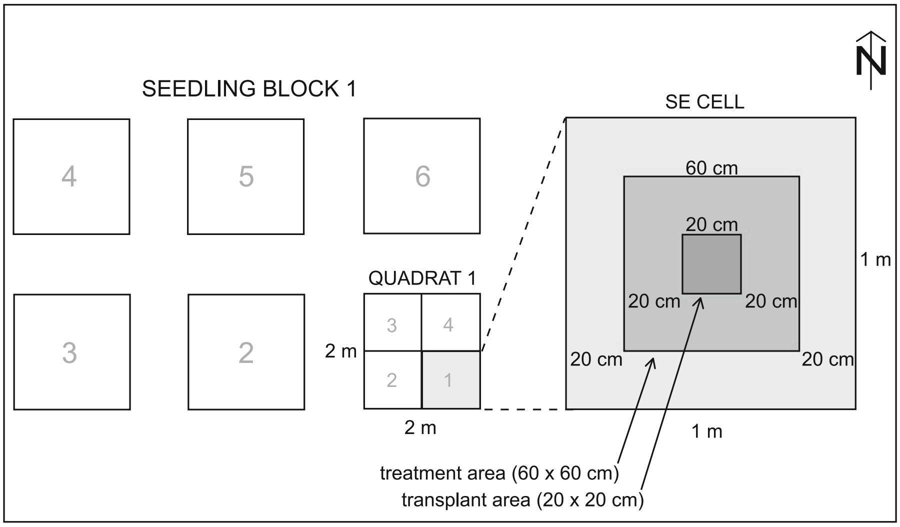

Fig. 1 Experimental design used to measure the impact of disturbance type and intensity on the invasibility of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. Four seedlings of smooth brome (*Bromus inermis* Leyss.) were transplanted into treatment areas at the center of 1 × 1 m quadrats used to quantify the impact of disturbance on invasibility. The four treatments (control, selective application of herbicide, simulated pocket gopher (*Thomomys talpoides*) disturbance, and non-selective application of herbicide), applied within six quadrats, were replicated within three experimental blocks, located in each of two prairies in the park ($n = 144$)

of prairie soil (0–15 cm deep × 5 cm wide, 74 cm^3), replacing each with one seedling, and backfilling each excavation with loose soil collected in the vicinity of the experimental blocks. For each prairie, all 576 seedlings were transplanted within a single evening. Previous attempts to germinate seeds directly inside the treatments failed. Transplanted seedlings were harvested in August 2004, at the end of one growing season. We clipped all seedlings at the soil surface and used a small spade to excavate their roots and rhizomes to a depth of 10 cm. All samples were oven dried (48 h, 60°C) before weighing; roots and rhizomes of *B. inermis* were washed using a mechanical root washer and separated by hand from those of other species. Although some of the transplanted seedlings were heavily browsed by animals, fewer than one percent (5/576) died during the experiment.

We monitored the impacts of disturbance on the structure and composition of prairie communities, as well as their soil moisture, temperature, and mineral nitrogen. During August 2004, prior to the harvest of transplanted seedlings, we estimated the foliar cover of species inside 0.5 × 0.5 m quadrats, centered inside each treatment cell. Foliar cover for each species was estimated using a 5% intervals and isolated individuals were assigned a cover of 0.5%. We also measured soil temperature and moisture inside each treatment cell (0–10 cm; HydroSense, Campbell Scientific Inc., Logan UT). Measurements of soil mineral nitrogen were based on in-situ incubation of mineral soil (Binkley and Hart 1989). Cores of soil, extracted using a hand auger (0–15 cm, 74 cm^3), were placed in plastic Ziploc bags and returned to the auger excavations between July and August 2004. Along with reference samples, collected at the start of the incubation, all samples were air dried, milled, extracted with 10% KCl, and analyzed for ammonium and nitrate using a Technicon Autoanalyzer (Maynard and Kalra 1993). As a result of rodent damage to the incubation bags, only the results from one prairie are presented here.

Statistical analysis

We used one-way analysis of variance (ANOVA), blocked by the six experimental blocks to account for variance among study sites, to examine the impacts of disturbance type and intensity on community invasibility. Using the mean above- and below-ground biomass and the maximum rhizome length of transplanted *Bromus inermis* seedlings inside each treatment cell, we tested the null hypothesis that prairie invasibility was independent of disturbance type and intensity. We calculated the effective richness, diversity, and evenness of disturbed communities, and compared their levels of available and mineralized nitrogen, soil moisture, and temperature. These were log transformed to improve the homogeneity of variance among treatment groups, while measurements of soil moisture, recorded as percentages, were arcsine transformed to approximate a normal distribution (Zar 1999). Effective richness $[N2 = (\Sigma p_i)^{-1}]$ and evenness $\{E3 = [(\Sigma p_i)^{-1}]/[\exp(\Sigma p_i \log p_i) - 1]\}$ describe plant communities based on the proportional abundance of species and the shape of their frequency distributions (Kvalseth 1991) and are helpful in examining species responses to environmental manipulations (Legendre and Legendre 1998). Differences in the composition of plant communities among disturbance types were also compared using canonical variate analysis (Legendre and Legendre 1998), based on the log transformed abundances of each species.

We used multiple regression models to examine the correlations between the establishment of *B. inermis* and the environments of disturbed communities. We eliminated the multicollinearity among variables with principal component analysis (Graham 2003), and used ordination scores along the first three component axes as predictors of the above- and below-ground biomass of transplanted seedlings. Best models were selected using the ‘step’ function, based on backward elimination of successive variables required to optimize the Akaike Information Criterion (AIC) of each model (R Development Core Team 2008). We selected models with the lowest AIC, but only if all coefficients in the model were significant (t-test: $P < 0.05$), and verified the automated function by calculating AIC values for all combinations of variables (“Appendix”). Univariate and multivariate statistical analyses were performed using R (R Development Core Team 2008) and SYNTAX 2000 (Podani 2001), respectively.

Results

Undisturbed prairies resisted the establishment of *Bromus inermis* more strongly compared to disturbed plots. Compared to other treatments, seedlings transplanted into undisturbed treatments accumulated little above- and belowground biomass and were characterized by short rhizomes (Fig. 2). Community invasibility increased with increasing disturbance. As a result, seedlings transplanted into areas treated selectively with herbicide, characterized by lower plant cover, effective richness and evenness (Table 1), accumulated more biomass and produced longer rhizomes (Fig. 2). This response was most pronounced where resident species had been eliminated with non-selective applications of herbicide (Fig. 2). Rapid recovery of prairie communities following burial with loose soil compromised the above- and below-ground biomass of *B. inermis* seedlings (Fig. 2). For example, despite the persistence of several ruderal species, including *Androsace septentrionalis* L. (pygmyflower), *Poa compressa* L. (Canada bluegrass) and *Stellaria longifolia* Muhl. (longleaf starwort), buried communities resembled undisturbed controls (Fig. 3). The first canonical axis, summarizing 85.8% of variance among treatment groups ($\lambda = 18.73$; $\chi^2_{210} = 499.93$, $P < 0.0001$), was strongly correlated with native perennials, including *Aster laevis* L. (smooth aster), *Gallium boreale* L. (northern bedstraw), and *Festuca hallii* (Vasey) Piper (Fig. 3).

The increasing invasibility of disturbed prairie communities was related to resource availability. Compared with undisturbed controls, both available and mineralized nitrogen increased with increasing disturbance (Table 1), and the negative covariance between soil nitrogen and plant diversity accounted for a high proportion of variance among quadrats (Fig. 4). The first principal component axis accounted for 52.2% ($\lambda = 5.74$) of variability among quadrats, with total and graminoid cover covarying positively with all indices of community diversity (all loadings ≥ 0.788) and opposite to mineral nitrogen, soil moisture, and the proportion of forbs (all loadings ≤ 0.428; Fig. 4). Differences in mineral nitrogen were also emphasized along the third component axis. Accounting for 9.7% of variance among samples ($\lambda = 1.06$), this axis separated treatments characterized by high evenness (loading = 0.451) and elevated levels of incubated nitrogen (loading = 0.660).

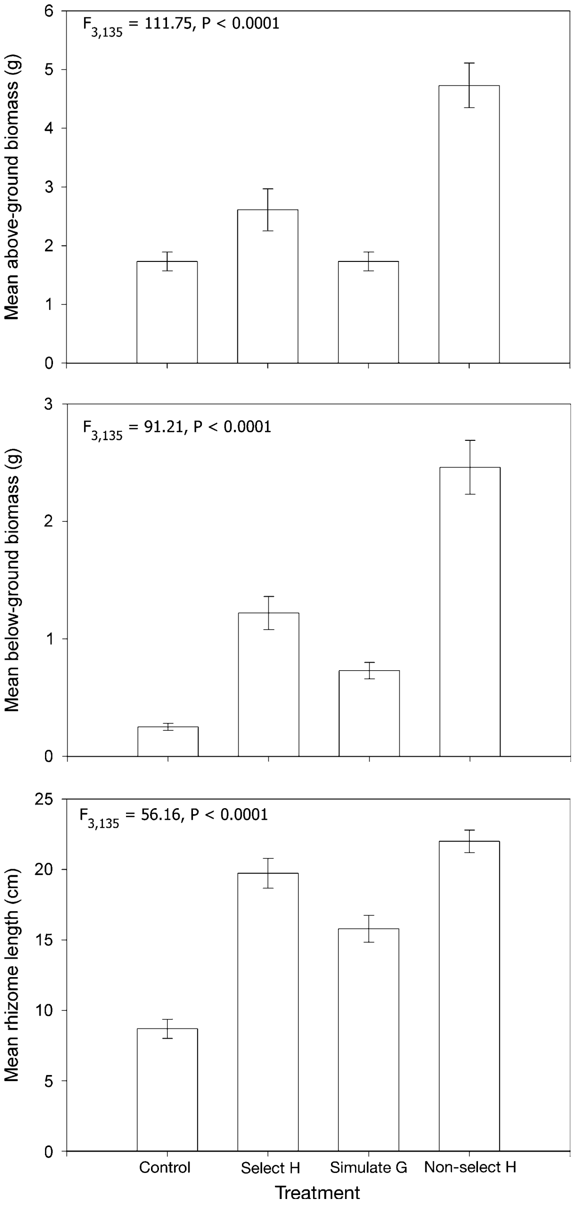

Fig. 2 Impacts of disturbance on the establishment of smooth brome (*Bromus inermis* Leyss.) seedlings, transplanted into northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, control, selective application of herbicide (Select H), simulated pocket gopher (*Thomomys talpoides*) disturbance (Simulate G), and non-selective application of herbicide (Non-select H), represent a gradient of disturbance type and intensity. Data represent the mean biomass and maximum rhizome length of four seedlings at the end of one growing season, and were blocked by the six experimental blocks to reduce variability among study areas within the one-way ANOVA model ($n = 144$). Means ± 1 SE

Table 1 Impacts of disturbance on the composition and the soil environments of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada

	Treatment				*F*	*df*	*P*
	Control	Select *H*	Simulate *G*	Non-select *H*			
Graminoids (%)	44.7 ± 3.5	7.6 ± 1.1	40.2 ± 4.1	2.8 ± 0.6	116.3	3,135	≤0.0001
Forbs (%)	83.0 ± 5.4	37.2 ± 5.2	79.4 ± 5.1	21.7 ± 2.9	93.8	3,135	≤0.0001
Total cover (%)	127.9 ± 8.01	44.8 ± 5.2	119.7 ± 7.7	24.5 ± 3.2	168.8	3,135	≤0.0001
Richness (*S*)	14.9 ± 0.5	7.7 ± 0.3	13.9 ± 0.4	5.2 ± 0.4	129.5	3,135	≤0.0001
Shannon's index [$N1 = \exp(-\Sigma p_i \log p_i)$]	2.87 ± 0.05	2.22 ± 0.04	2.78 ± 0.05	1.90 ± 0.06	88.5	3,135	≤0.0001
Effective richness [$N2 = (\Sigma p_i^2)^{-1}$]	9.46 ± 0.37	5.52 ± 0.32	8.89 ± 0.38	4.22 ± 0.32	57.6	3,135	≤0.0001
Evenness [$E3 = (N2-1)/(N1-1)$]	4.45 ± 0.1	3.58 ± 0.13	4.31 ± 0.12	3.36 ± 0.12	20.8	3,135	≤0.0001
Soil moisture (%)	16.6 ± 0.7	16.9 ± 0.8	14.6 ± 0.6	18.3 ± 0.7	7.7	3,135	≤0.0001
Soil temperature (°C)	12.8 ± 0.1	13.4 ± 0.2	13.8 ± 0.3	13.3 ± 0.2	10.8	3,135	≤0.0001
Available nitrogen (mg kg^{-1})[a]	17.65 ± 1.49	25.25 ± 1.81	14.63 ± 0.67	24.95 ± 2.18	15.2	3,69	≤0.0001
Mineralized nitrogen (mg kg^{-1})[a]	14.02 ± 4.06	32.33 ± 5.05	21.77 ± 5.50	52.51 ± 10.78	1.51	3,69	≤0.0001

The treatments, control, selective application of herbicide (Select H), simulated pocket gopher (*Thomomys talpoides*) disturbance (Simulate G), and non-selective application of herbicide (Non-select H), represent a gradient of disturbance type and intensity and were applied 1 year prior to surveys within six quadrats, replicated within three experimental blocks, located in each of two prairies in the park ($n = 144$). Measurements of soil moisture (0–10 cm; HydroSense, Campbell Scientific Inc., Logan UT) were collected during August 2004. Available and mineralized nitrogen were based on samples of soil (0–15 cm), air dried, milled and extracted using 10% KCl. Mineralized nitrogen describes samples of mineral soil (0–15 cm), incubated in-situ between July and August 2004 (see text for details). As a result of rodent damage to the incubation bags, only the results from one prairie are presented here ($n = 72$). Data were log transformed and the means of treatment groups were blocked by the six experimental blocks to reduce variability among study areas within the one-way ANOVA model. Means ± 1 SE

[a] $[NH_4^+ N] + [NO_3^- N]$

Community diversity and soil mineral nitrogen accounted for a large proportion of variance in the aboveground biomass of smooth brome seedlings ($R^2 = 0.593$, $F_{2,67} = 51.2$, $P < 0.001$). Seedling biomass was correlated negatively with plant diversity, increasing along the first principal component axis ($\beta = -0.088$, $t = -9.2$, $P < 0.001$), and positively with soil nitrogen increasing along the third component axes ($\beta = 0.091$, $t = 4.1$, $P < 0.001$; Table 2). Similar responses were observed in the belowground biomass of seedlings (Table 2).

Discussion

Our observations of northern fescue prairies demonstrate that their vulnerability to exotic plant invasions is contingent on disturbance. While the establishment of smooth brome seedlings increased with increasing disturbance, its impact depended on the availability of soil nitrogen. Above and below-ground, brome biomass increased in response to greater nitrogen mineralization, characteristic of more disturbed, low diversity communities, however, establishment of brome seedlings remained contingent on disturbance type. Burial treatments, simulating the disturbance caused by northern pocket gophers, provided poor recruitment areas for smooth brome, and their low levels of soil moisture and nitrogen, combined with the rapid recovery of the prairie community, compromised seedling establishment.

Covariance between disturbance and soil resources

Understanding the impacts of diversity on community resistance to exotic invasions is complicated by the fact that changes in diversity covary with factors known to influence invasibility (Levine and D'Antonio 1999). While aboveground, changes in the structure and composition of native communities also affect their invasibility (Crawley 1987), the impacts of plant diversity on the niche opportunities available to potential invaders can be equally acute belowground

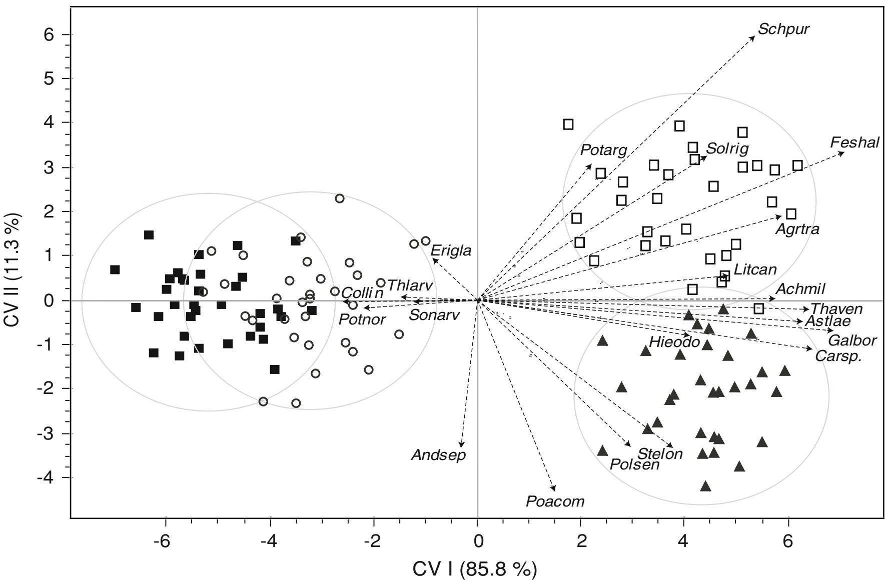

Fig. 3 Impacts of disturbance on the composition of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, control (□), selective application of herbicide (◯), simulated pocket gopher (*Thomomys talpoides*) disturbance (▲), and non-selective application of herbicide (■) represent a gradient of disturbance type and intensity, and were applied within six quadrats, replicated within three experimental blocks, located in each of two prairies in the park ($n = 144$). For clarity, only those species contributing substantially to each canonical variate axis were included. Eigenvectors have been normalized to unit length resulting in spherical dispersions of group objects; the illustrated isodensity circles contain 95% of the individuals belonging to each group (Podani 2001). Abbreviations: Achmil (*Achillea millefolium*), Agrtra (*Agropyron trachycaulum*), Andsep (*Andosace septentrionalis*), Astlae (*Aster laevis*), Carsp. (*Carex* sp.), Collin (*Collomia linearis*), Erigla (*Erigeron glabellus*), Feshal (*Festuca halii*), Galbor (*Galium boreale*), Hieodo (*Hierochloe odorata*), Litcan (*Lithospermum canescens*), Poacom (*Poa compressa*), Polsen (*Polygala senega*), Potarg (*Potentilla arguta*), Potnor (*P. norvegica*), Schpur (*Schizachne purpurascens*), Solrig (*Solidago rigida*), Sonarv (*Sonchus arvensis*), Stelon (*Stellaria longifolia*), Thaven (*Thalictrum venulosum*), Thlarv (*Thlaspi arvense*). Nomenclature according to the Great Plains Flora Association (1986)

(Lamb 2008). Our results demonstrate that increasing disturbance corresponds with higher rates of nitrogen mineralization, a likely response to higher soil moisture and temperature of disturbed, low diversity communities as well as the increased mineralization of plant biomass killed by herbicide. Increasing soil nitrogen following a decline in plant diversity has been observed in other studies. For example, Tilman et al. (1996) correlated the higher number of species in experimental prairie plots with lower concentrations of inorganic soil nitrogen. While the mechanisms underlying the inverse relationship between diversity and resource availability remain unclear (Chapin et al. 1998), the efficiency of resource use is central to both the niche complementarity and sampling effect hypotheses invoked to explain these observations (Tilman 1999).

Although our results demonstrate the impact of disturbance on community diversity, soil resources, and the invasibility of prairie communities, disturbance is not pre-requisite for successful invasions (Usher 1988; Lodge 1993). For example, the degree of niche overlap between the native and non-native species may determine the pattern and extent of invasion (Hoopes and Hall 2002). As a result, exotic species with broad ecological niches or wide dispersal may become prolific invaders regardless of disturbance (Lodge 1993; Silvertown et al. 1999; Buckling et al. 2000). Equally important may be the extent of environmental heterogeneity and its ability to facilitate the coexistence of a higher number of resident species (Melbourne et al. 2007).

Impacts of disturbance on community diversity

Understanding community resistance to invasions is imperative to the conservation and restoration of natural ecosystems (Chapin et al. 1998). Although the potential mechanisms responsible for the stability of

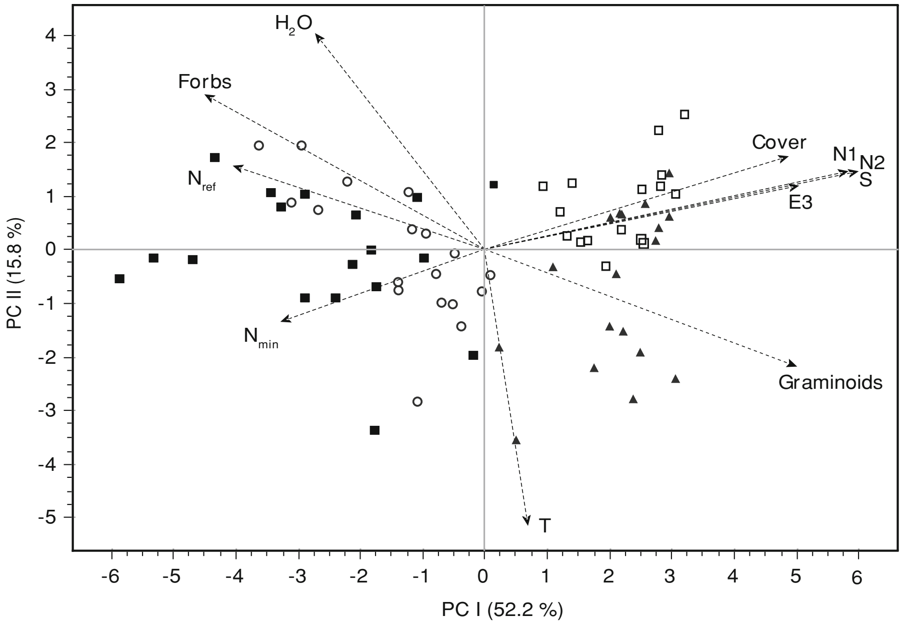

Fig. 4 Covariance between the impacts of disturbance and plant diversity manipulations and the function of northern fescue prairies in Riding Mountain National Park, Manitoba, Canada. The treatments, control (□), selective application of herbicide (○), simulated pocket gopher (*Thomomys talpoides*) disturbance (▲), and non-selective application of herbicide (■) represent a gradient of disturbance type and intensity, and were applied within six quadrats, replicated within three experimental blocks, located in each of two prairies in the park. As a result of rodent damage to the incubation bags, only the results from one prairie are presented here ($n = 72$). Graminoids and forbs represent their proportional contribution to total plant community cover. Community richness (S), Shannon's diversity ($N1$), Effective richness ($N2$), and evenness ($E3$) summarize differences in plant community composition among disturbance treatments, while soil moisture (H_2O), temperature (T), mineral (N_{ref}) and incubated nitrogen (N_{min}) describe the covariance between changes in plant community composition and soil environments. All variables were log transformed

Table 2 Impacts of disturbance on the above- and below-ground biomass of smooth brome (*Bromus inermis* Leyss.), invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada

Dependent variable	Predictor	Parameter estimate	SE	*t*	*P*	Model			
						F	*df*	*P*	Adj. R^2
Above-ground biomass	Intercept	0.484	0.023	21.431	<0.0001	34.3	2,67	<0.0001	0.593
	PC 1	−0.088	0.009	−9.251	<0.0001				
	PC 3	0.091	0.022	4.121	<0.0001				
Below-ground biomass	Intercept	0.310	0.021	14.952	<0.0001	30.68	2,67	<0.0001	0.462
	PC 1	−0.061	0.009	−6.957	<0.0001				
	PC 3	0.073	0.020	3.596	<0.0001				

Model variables represent principal component scores from an ordination of plant community and soil environments and were selected based on backward elimination to optimize the Akaike Information Criterion (AIC) of each model (R Development Core Team 2008). See "Appendix" for all tested combinations of variables

diverse communities remain elusive (Levine and D'Antonio 1999), the ability of species to reduce resource fluctuations is likely a key element (McCann 2000). The importance of disturbance in community invasibility suggests that invasions are most likely when one or more species are compromised (Hutchinson 1959). While our results, demonstrating the impact of disturbance on community diversity and the invasibility of northern fescue prairies, support these observations, important distinctions in the structure and composition of resident communities remain unaddressed. For example, the strong covariance between species richness, evenness, and total plant cover complicate evaluating their individual contribution to invasibility (Mattingly et al. 2007). As a result, it remains unresolved whether plant communities characterized by the high cover of a small number of species are as invasible as those with a greater diversity of residents. Perhaps, invaded communities, dominated by a small number of exotic species can provide a valuable system to study this important question.

Even though diverse communities are more likely to include competitive species that resist potential invaders (Huston 1997; Wardle 2001), compensation and greater variance of responses by a small number of species may also enable the maintenance of community productivity and continued resistance to potential invaders (Chapin et al. 1998). As a result, even low diversity patches may resist invaders given their dominance by one or few highly competitive species (Levine and D'Antonio 1999). The fact that highly competitive or functionally similar species contribute disproportionally to the invasion resistance of diverse communities (Tilman 1997) raises important questions about the direction of character displacement in communities subjected to disturbance. To our knowledge, these questions remain unanswered.

Impact of disturbance type on community recovery

The impact of disturbance on the invasibility of native plant communities remains contingent on disturbance type. Based on our observations, simulated pocket gopher mounds provided poor recruitment areas for the establishment of smooth brome seedlings. While several authors have demonstrated successful recruitment of exotic plants inside gopher mounds as well as areas of bare ground (Hobbs and Mooney 1985; D'Antonio 1993; Symstad 2000), the observed discrepancies may be attributable to differences in environmental conditions (Koide et al. 1987). For example, Laycock (1958) reported low germination of plants colonizing gopher mounds in areas of low soil moisture and emphasized the importance of mound thickness in the regeneration of buried plants. Among others, thickness of the deposit as well as its origin in the soil profile may also impact plant regrowth and establishment through their influence on moisture and nutrient concentrations (Weaver and Fitzpatrick 1934; Koide et al. 1987). While our observations of community recovery following burial are corroborated by other studies (Sherrod et al. 2005), our results also stress the importance of disturbance type on community invasibility. As a result, disturbances that preserve the root and rhizome function of native species, including burial by pocket gophers, may be less vulnerable to exotic invaders than those where the root function has been compromised. The integrity of belowground biomass may constitute an important and often overlooked component of community diversity, the maintenance and restoration of which may be key in the ability of ecosystems to resist biological invaders.

Impacts of disturbance and resources on community invasibility depend on the life history of potential invaders (Renne et al. 2006). While we demonstrate the impacts of disturbance on the establishment of smooth brome, factors that determine the dispersal and proliferation of established populations remain key in the prediction and management of potential invasions (Davis et al. 2000; Larson 2003). For example, the rapid initiation of rhizomes by seedlings established inside simulated pocket gopher mounds illustrates their continued threat to adjacent prairie communities. Despite their low biomass, clonal expansion by seedlings established in burial treatments could facilitate their proliferation into adjacent prairie communities (Otfinowski and Kenkel 2008). Equally important in predicting biological invasions may be impacts of multi-trophic interactions (Klironomos 2002; Callaway et al. 2004) and the important role of dispersal in initiating and compensating the potential inverse density dependence among invading populations (Sakai et al. 2001). Such factors emphasize the importance of considering several stages in the life history of potential invaders (Dietz and Edwards 2006) as well as a clear definition of their invasion success (Levine and D'Antonio 1999).

Globally, few habitats remain free of exotic species, and many pose serious threats to the biodiversity and function of native ecosystems (Ricciardi 2007). Our results confirm that niche opportunities afforded to potential invaders, may be central to the frequently conflicting results of studies examining the role of diversity in community invasibility (Levine and D'Antonio 1999; Davis et al. 2000). Emphasizing the impact of disturbance on community diversity and resource opportunities, our findings also illustrate the importance of disturbance type in the invasibility of native prairies. Such a consideration is critical in the conservation and restoration of natural areas and maintaining their resistance to exotic invaders.

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Appendix

See Table 3.

Table 3 Results of linear regression models for the above- and belowground biomass of smooth brome (*Bromus inermis* Leyss.), invading northern fescue prairies in Riding Mountain National Park, Manitoba, Canada

Dependent variable	Predictor	Parameter estimate	SE	*t*	*P*	Model				
						F	*df*	*P*	Adj. R^2	AIC
Above-ground biomass	Intercept	0.484	0.025	19.290	<0.0001	69.31	1,68	<0.0001	0.498	−15.81
	PC 1	−0.088	0.010	−8.325	<0.0001					
	Intercept	0.484	0.035	13.580	<0.0001	0.08	1,68	<0.0001	−0.013	33.30
	PC 2	−0.008	0.027	−0.282	0.7790					
	Intercept	0.484	0.034	14.308	<0.0001	7.58	1,68	0.0076	0.100	25.99
	PC 3	0.091	0.033	2.753	0.0076					
	Intercept	0.484	0.025	19.165	<0.0001	34.3	2,67	<0.0001	0.491	−13.97
	PC 1	−0.088	0.010	−8.273	<0.0001					
	PC 2	−0.008	0.019	−0.393	0.6960					
	Intercept	0.484	0.023	21.431	<0.0001	34.3	2,67	<0.0001	0.593	−29.62
	PC 1	−0.088	0.009	−9.251	<0.0001					
	PC 3	0.091	0.022	4.121	<0.0001					
	Intercept	0.484	0.034	14.211	<0.0001	3.78	2,67	0.0278	0.074	27.90
	PC 2	−0.008	0.026	−0.295	0.7699					
	PC 3	0.091	0.033	2.734	0.0080					
	Intercept	0.484	0.023	21.301	<0.0001	33.85	3,66	<0.0001	0.588	−27.83
	PC 1	−0.008	0.009	−9.195	<0.0001					
	PC 2	−0.008	0.017	−0.436	0.6641					
	PC 3	0.091	0.022	4.096	0.0001					
Below-ground biomass	Intercept	0.310	0.022	13.791	<0.0001	41.19	1,68	<0.0001	0.368	−31.45
	PC 1	−0.061	0.009	−6.418	<0.0001					
	Intercept	0.310	0.028	10.889	<0.0001	0.06	1,68	0.8080	−0.014	1.64
	PC 2	0.005	0.021	0.244	0.8080					
	Intercept	0.310	0.027	11.478	<0.0001	7.62	1,68	0.0074	0.088	−5.74
	PC 3	0.073	0.027	2.762	0.0074					
	Intercept	0.310	0.023	13.699	<0.0001	20.37	2,67	<0.0001	0.360	−29.55
	PC 1	−0.061	0.009	−6.375	<0.0001					
	PC 2	0.005	0.017	0.311	0.7570					
	Intercept	0.310	0.021	14.952	<0.0001	30.68	2,67	<0.0001	0.462	−41.81

Table 3 continued

Dependent variable	Predictor	Parameter estimate	SE	*t*	*P*	Model				
						F	*df*	*P*	Adj. R^2	AIC
	PC 1	−0.061	0.009	−6.957	<0.0001					
	PC 3	0.073	0.020	3.596	<0.0001					
	Intercept	0.310	0.027	11.398	<0.0001	3.79	2,67	0.0275	0.075	−3.81
	PC 2	0.005	0.021	0.256	0.7990					
	PC 3	0.073	0.027	2.743	0.0078					
	Intercept	0.310	0.021	14.852	<0.0001	20.22	3,66	<0.0001	0.455	−39.92
	PC 1	−0.061	0.009	−6.911	<0.0001					
	PC 2	0.005	0.016	0.338	0.7367					
	PC 3	0.073	0.020	3.573	<0.0001					

Model variables represent principal component scores from an ordination of plant community and soil environments. See the text for details. The Akaike Information Criterion (AIC) for each model was calculated using the 'AIC' function in 'R' (R Development Core Team 2008)

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